



## Historic 2005 toxic bloom of *Alexandrium fundyense* in the western Gulf of Maine:

### 2. Coupled biophysical numerical modeling

Ruoying He,<sup>1</sup> Dennis J. McGillicuddy Jr.,<sup>2</sup> Bruce A. Keafer,<sup>3</sup> and Donald M. Anderson<sup>3</sup>

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[1] A coupled physical/biological modeling system was used to hindcast a massive *Alexandrium fundyense* bloom that occurred in the western Gulf of Maine in 2005 and to investigate the relative importance of factors governing the bloom's initiation and development. The coupled system consists of a state-of-the-art, free-surface primitive equation Regional Ocean Modeling System (ROMS) tailored for the Gulf of Maine (GOM) using a multinested configuration, and a population dynamics model for *A. fundyense*. The system was forced by realistic momentum and buoyancy fluxes, tides, river runoff, observed *A. fundyense* benthic cyst abundance, and climatological nutrient fields. Extensive comparisons were made between simulated (both physical and biological) fields and in situ observations, revealing that the hindcast model is capable of reproducing the temporal evolution and spatial distribution of the 2005 bloom. Sensitivity experiments were then performed to distinguish the roles of three major factors hypothesized to contribute to the bloom: (1) the high abundance of cysts in western GOM sediments; (2) strong 'northeaster' storms with prevailing downwelling-favorable winds; and (3) a large amount of fresh water input due to abundant rainfall and heavy snowmelt. Model results suggest the following. (1) The high abundance of cysts in western GOM was the primary factor of the 2005 bloom. (2) Wind-forcing was an important regulator, as episodic bursts of northeast winds caused onshore advection of offshore populations. These downwelling favorable winds accelerated the alongshore flow, resulting in transport of high cell concentrations into Massachusetts Bay. A large regional bloom would still have happened, however, even with normal or typical winds for that period. (3) Anomalously high river runoff in 2005 resulted in stronger buoyant plumes/currents, which facilitated the transport of cell population to the western GOM. While affecting nearshore cell abundance in Massachusetts Bay, the buoyant plumes were confined near to the coast, and had limited impact on the gulf-wide bloom distribution.

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### 1. Introduction

[2] In summer 2005 the Gulf of Maine (GOM) experienced the largest toxic bloom of *Alexandrium fundyense* in at least 33 years [Anderson *et al.*, 2005]. The bloom posed a serious human health threat due to the accumulation of neurotoxins in shellfish that feed on *A. fundyense* cells, resulting in a potentially fatal illness known as paralytic

shellfish poisoning (PSP). During this event, GOM hydrography, circulation, and surface momentum and buoyancy forcing were all found to be anomalous, some aspects of which may have contributed to the bloom and its impact along the coast [He and McGillicuddy, 2008]. Biological factors may have played an important role as well, as *A. fundyense* has unique life history characteristics that lead to complicated bloom dynamics. Anderson [1998] summarized the life history of *A. fundyense*, which includes both a resting cyst and a planktonic phase of vegetative growth. In particular, cyst germination is the key process that initiates recurrent blooms that are self-seeding and propagatory in nature, supplying cells that populate the GOM [Anderson *et al.*, 2005] As such, the timing, intensity, and spatial distribution of blooms of this meroplanktonic dinoflagellate are determined collectively by complex interactions between the physical environment and biological processes.

<sup>1</sup>Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina, USA.

<sup>2</sup>Department of Applied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA.

<sup>3</sup>Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA.

[3] While in situ observations provide valuable clues to physical and biological factors that may have been important for the 2005 bloom event, they are too sparse to depict the full space-time evolution of the bloom and to reveal the underlying circulation and bloom dynamics. In this regard, numerical model simulations offer a means by which detailed mechanisms regulating bloom initiation and development can be examined. Prior modeling studies have investigated various aspects of the *A. fundyense* dynamics in detail. *Stock et al.* [2005,2007] examined the factors governing the initiation and development of *A. fundyense* blooms in the western GOM during springs of 1993 and 1994. In those studies, coastal circulation was simulated using a three-dimensional Princeton Ocean model forced by climatological boundary conditions and observed winds, heat flux, and river discharge. It was coupled with an *A. fundyense* population dynamics submodel constructed from laboratory and field data that estimates the germination and growth rates of *A. fundyense* as a function of ambient environmental conditions [*Anderson et al.*, 2005]. *McGillicuddy et al.* [2005] coupled the same *A. fundyense* submodel with GOM climatological seasonal mean flow. Simulated bloom conditions matched observations reasonably well, and were used to analyze the mechanisms regulating the mean large-scale seasonal fluctuations of the *A. fundyense* population.

[4] Our goal in the present study is to apply an improved coupled physical-biological model that considers realistic surface and open boundary conditions to hindcast the massive *A. fundyense* bloom in 2005. On the basis of a combination of physical and biological observations, *Anderson et al.* [2005] hypothesized that three factors may have contributed to this record bloom: (1) strong northeasterly wind that facilitated onshore transport of offshore cell populations; (2) high river runoff, which increased the water stratification, and southwestward transport via buoyant coastal plume, as well as enhancing growth conditions via nutrient supply; and (3) high abundance of *A. fundyense* cysts in the GOM sediments (the western GOM in particular), which provided an enhanced source population. Our objective here is therefore to test these three hypotheses by performing model sensitivity experiments to differentiate and quantify the relative importance of these factors in regulating the 2005 bloom.

## 2. Methods

[5] Our coupled modeling system consists of a circulation model and an *A. fundyense* population dynamics model. These two models are linked together by advection and mixing, for which the physical model passes 3-day velocity and turbulence diffusivity fields to the biological model.

### 2.1. Circulation Modeling

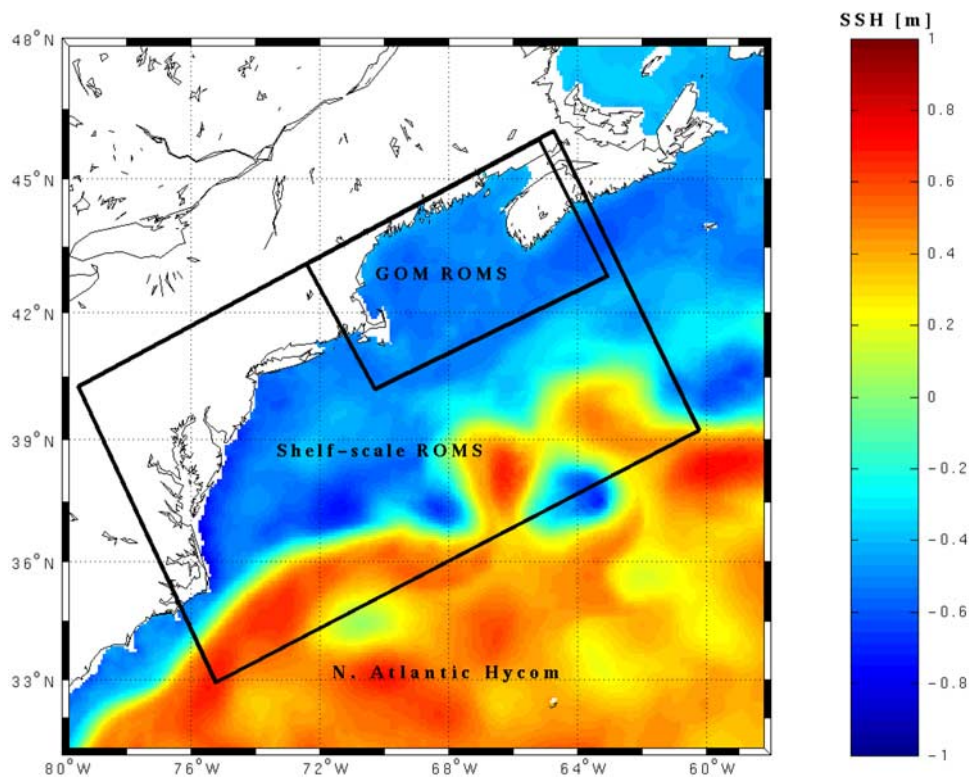
[6] The coastal circulation simulations was performed using the Regional Ocean Modeling System (ROMS), a free-surface, hydrostatic, primitive-equation model in widespread use for estuarine, coastal and shelf-wide applications [e.g., *Dinniman et al.*, 2003; *Lutjeharms et al.*, 2003; *MacCready and Geyer*, 2001; *Marchesiello et al.*, 2001; *Peliz et al.*, 2003]. ROMS employs split-explicit separation of fast barotropic and slow baroclinic modes, and is formulated in vertically stretched terrain-following coordi-

nates using algorithms described in detail by *Shechepetkin and McWilliams* [1998, 2003, 2005]. The ROMS computational kernel includes high-order advection and time stepping schemes, weighted temporal averaging of the barotropic mode to reduce aliasing into the slow baroclinic motions, and conservative parabolic splines for vertical discretization. A redefinition of the barotropic pressure-gradient term is also applied in ROMS to reduce the pressure-gradient truncation error, which has previously limited the accuracy of terrain-following coordinate models.

[7] To overcome the difficulties associated with defining open boundary conditions for a regional coastal circulation model, we implemented a multinested configuration (Figure 1), which allows direct connection between the north Atlantic basin-scale circulation with the targeted GOM coastal circulation. The North Atlantic (NA) circulation hindcasts were provided by Naval Research Laboratory and University of Miami using the Hybrid Coordinate Ocean Model (HYCOM). As part of the Global Ocean Data Assimilation Experiment (GODAE), the NA-HYCOM assimilates satellite observed sea surface temperature and sea surface heights, providing daily best estimates of North Atlantic Circulation at  $\sim 10$  km resolution (<http://hycom.rsmas.miami.edu/dataserver>).

[8] Inside HYCOM, we nested a shelf-scale ROMS, which encompasses both the Gulf of Maine (GOM) and the Middle Atlantic Bight (MAB). Horizontal resolution varies from 5 km near the coast to 10 km in the deep ocean. Vertically, there are 36 terrain-following sigma levels in the water column with higher resolution near the surface and bottom in order to better resolve boundary layers. A one-way nesting approach was used to connect shelf-scale ROMS with the basin-scale HYCOM. Specifically, open boundary conditions (OBCs) were applied to tracers and baroclinic velocity following the method of *Marchesiello et al.* [2001], whereby Orlanski-type radiation conditions were used in conjunction with relaxation (with timescale of 0.5 days on inflow and 10 days on outflow) to HYCOM solutions. Free surface and depth-integrated velocity boundary conditions were specified using the method of *Flather* [1976] with the external values provided by HYCOM. Because HYCOM does not currently include tidal forcing, tidal harmonics from an ADCIRC simulation of the western Atlantic [*Luettich et al.*, 1992] were superimposed on the OBCs. Analysis of the interior solution confirmed the approach yielded accurate tidal predictions as compared with earlier studies [e.g., *Moddy et al.*, 1984; *Xue and Pettigrew*, 2000]. We applied the method of *Mellor and Yamada* [1982] to compute vertical turbulent mixing, as well as the quadratic drag formulation for the bottom friction specification. The same one-way nesting approach and OBC treatment were then applied to downscale the shelf-scale (GOM-MAB) circulation to the innermost model for the GOM. The GOM ROMS model has a spatial resolution ranging from 1 km near the coast to 3 km in the offshore gulf water. There are also 36 layers in the vertical having the same resolution distribution as the shelf-scale GOM-MAB ROMS.

[9] Distinctive advantages of such multinested configuration include: (1) it allows us to account for the impacts of upstream and deep-ocean forcing on the GOM circulation in a dynamically consistent and quantitatively accurate manner; and (2) the high resolution enables the GOM ROMS to



**Figure 1.** Multinested configuration for the regional GOM circulation and *A. fundyense* bloom modeling. The outermost model is the data assimilative North Atlantic HYCOM, which provides open boundary conditions (OBCs) for the shelf-scale ROMS model, which in turn provides OBCs for the innermost Gulf of Maine ROMS model.

resolve important small-scale coastal dynamics (e.g., river plumes), which are critical for resolving the transport and distribution of *A. fundyense* population. Prior experience with regional models in the Gulf of Maine suggests significant improvement in skill can be achieved through accurate specification of the open boundary condition [He et al., 2005].

[10] Given the nature of one-way nesting, model hindcasts were performed in a sequential order. The nested shelf-scale GOM-MAB ROMS hindcast was performed first, in which only the hydrodynamics was computed; then with OBCs from shelf-scale ROMS, the nested GOM ROMS hindcast was carried out, in which both hydrodynamics and the *A. fundyense* cell concentration were simulated simultaneously. Both the shelf-scale GOM-MAB ROMS and GOM ROMS hindcasts started on March 1st and ended on September 1st, 2005. Initial hydrodynamic conditions for both simulations were taken from HYCOM best estimate conditions for 1 March 2005.

## 2.2. *A. fundyense* Population Dynamics Model

[11] The *A. fundyense* submodel is a single-component biological model containing parameterizations of *A. fundyense* germination, growth, swimming behavior, and mortality. Fundamental to *A. fundyense* modeling approach is the concept that the ecosystem in which *A. fundyense* resides is not explicitly modeled. This is justified on the basis that *A. fundyense* generally constitutes only a small fraction of the phytoplankton assemblage in the GOM [McGillicuddy et

al., 2005]. As such, although blooms of *A. fundyense* display considerable interannual variation in terms of their occurrence and magnitude, they are a minor component of GOM phytoplankton community and presumably have little effect on ambient conditions such as nutrient concentration [Love et al., 2005] and the abundance of predators.

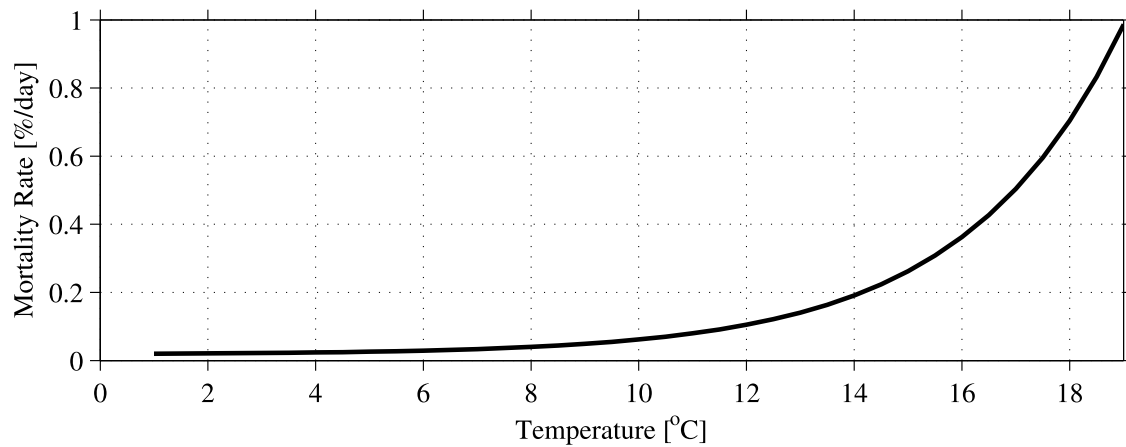
[12] The evolution of *A. fundyense* can be expressed as an advection-diffusion-reaction equation:

$$\frac{\partial C}{\partial t} + (\bar{u} + w_a) \cdot \nabla C = \nabla \cdot K \nabla C + (\mu - m)C + F_g$$

where  $C$  is the concentration of *A. fundyense*,  $\bar{u}$  and  $w_a$  are the fluid velocity and *A. fundyense* upward swimming velocity;  $K$  is the diffusivity,  $\mu$  and  $m$  are the cell growth and mortality terms respectively, and  $F_g$  is the germination flux from the sediment layer (cyst stage) to the water column (vegetative cell stage). The rate of *A. fundyense* growth  $\mu$  is dependent on temperature, salinity, and irradiance and nutrient concentration. Swimming velocity  $w_a$  is set at  $10 \text{ mday}^{-1}$ , a value determined by laboratory work in early studies [e.g., Anderson and Stolzenbach, 1985; Kamykowski et al., 1992; MacIntyre et al., 1997]. Interested readers are referred to Stock et al. [2005] for detailed description of the model and parameterizations for  $\mu$ ,  $w_a$ ,  $m$  and  $F_g$ .

[13] The *A. fundyense* submodel used in this study includes one important improvement on the Stock et al. [2005] formulation. Rather than using a constant average rate of mortality, we allowed  $m$  to vary with ambient water





**Figure 2.** Improved mortality function used in the *A. fundyense* population dynamics model.

temperature  $T$  on the basis of the  $Q_{10}$  formulation [Durbin and Durbin, 1992]:

$$m = a \cdot Q_{10}^{((T-10.35)/10)}, \text{ where } a = 0.066, \text{ and } Q_{10} = 21.75$$

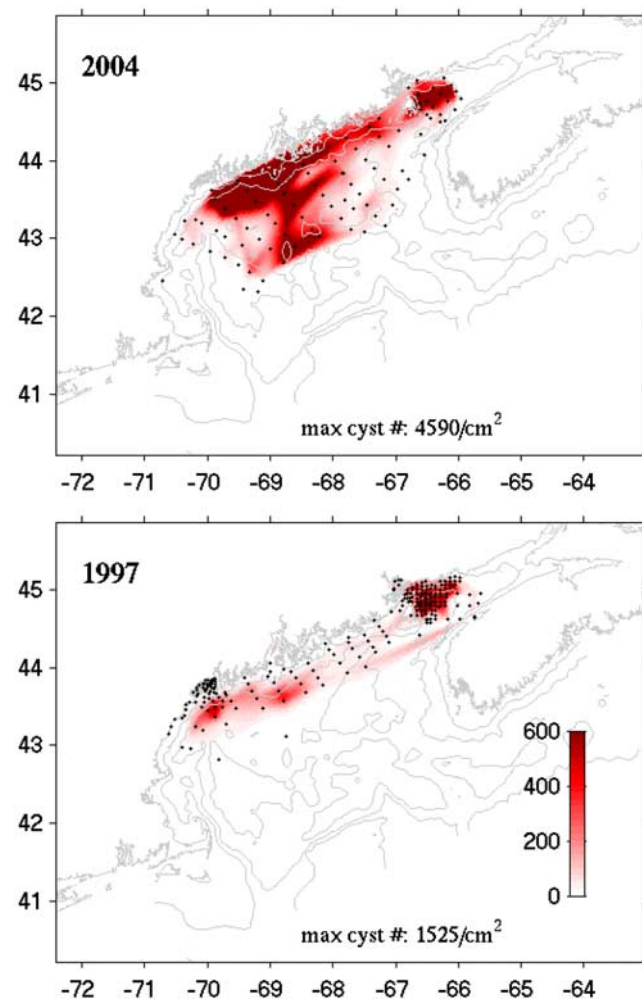
The underlying assumption is that activity of *A. fundyense*'s predators will increase with temperature (Figure 2), just as the growth rate of *A. fundyense* increases with temperature (albeit formulated in a different manner [see Stock et al., 2005]). This parameterization of temperature-dependent mortality was found to be more effective in capturing the late-season demise of the bloom, during which loss processes are apparently accelerated. However, this formulation still remains a vast simplification of the suite of loss processes including predation, cell mortality, and encystment. Improved representation of these effects is a topic of ongoing research.

[14] The initial *A. fundyense* concentration was set to zero everywhere. The distribution of benthic cysts was specified from sediment core surveys (Figure 3) conducted in fall 2004 (central hindcast) and fall 1997 (sensitivity experiment) respectively, and we assume over-winter loss of cysts is negligible before germination begins the following spring. Because no information was available to specify cell concentration along model open boundaries, we applied no-gradient OBCs for *A. fundyense* at all three GOM ROMS boundaries throughout the simulation. Similarly, the numbers of in situ nutrient observations in 2005 were insufficient to specify the time evolution of the three-dimensional nutrient (dissolved inorganic nitrogen, or DIN) fields, so we used the nutrient climatology described by Petrie et al. [1999], linearly interpolated between quarterly fields (15 February, 15 May, 15 August and 15 November) provided by that database.

### 2.3. Forcing

[15] Table 1 lists the forcing functions used in the model simulations. For both the shelf-scale MAB-GOM ROMS and GOM ROMS hindcasts, surface atmospheric conditions from National Oceanic and Atmospheric Administration (NOAA)'s Air Quality Research Lab (ARL) EDAS archive (<http://www.arl.noaa.gov/ss/transport/archives.html>) were utilized. The spatial resolution of this archive is 40 km. Air-sea fluxes of heat and momentum were computed by applying the standard bulk formulae [Fairall et al., 2003] to

EDAS marine boundary layer winds, air temperature, relative humidity, air pressure, and ROMS generated sea surface temperature (SST) and surface currents. In addition, the EDAS solar radiation field was also used in the



**Figure 3.** Comparison of benthic cyst distribution and abundance between (top) 2004 and (bottom) 1997. The 2004 cyst abundance data was used to produce the central hindcast of 2005 *A. fundyense* bloom.



**Table 1.** Surface and Boundary Forcing Elements Used in the Coupled Physical-Biological Model Hindcast

	Details
Major tidal constituents	$M_2$ , $S_2$ , $N_2$ , $K_2$ , $K_1$ , $O_1$ , $Q_1$
Surface Forcing	6-hr wind stress and heat flux computed with NOAA ARL EDAS archive
River runoff	Near real-time USGS river gauge data
Open boundary conditions	“Parent” model solutions

*A. fundyense* growth model. Real-time river runoff time series from United State Geological Survey (USGS) were collected to specify freshwater input into the GOM. As tides are important circulation component in this coastal region, the 7 major tidal constituents ( $M_2$ ,  $S_2$ ,  $N_2$ ,  $K_2$ ,  $K_1$ ,  $O_1$ ,  $Q_1$ ) were introduced by superimposing tidal harmonics on subtidal OBCs using the *Flather* [1976] boundary condition.

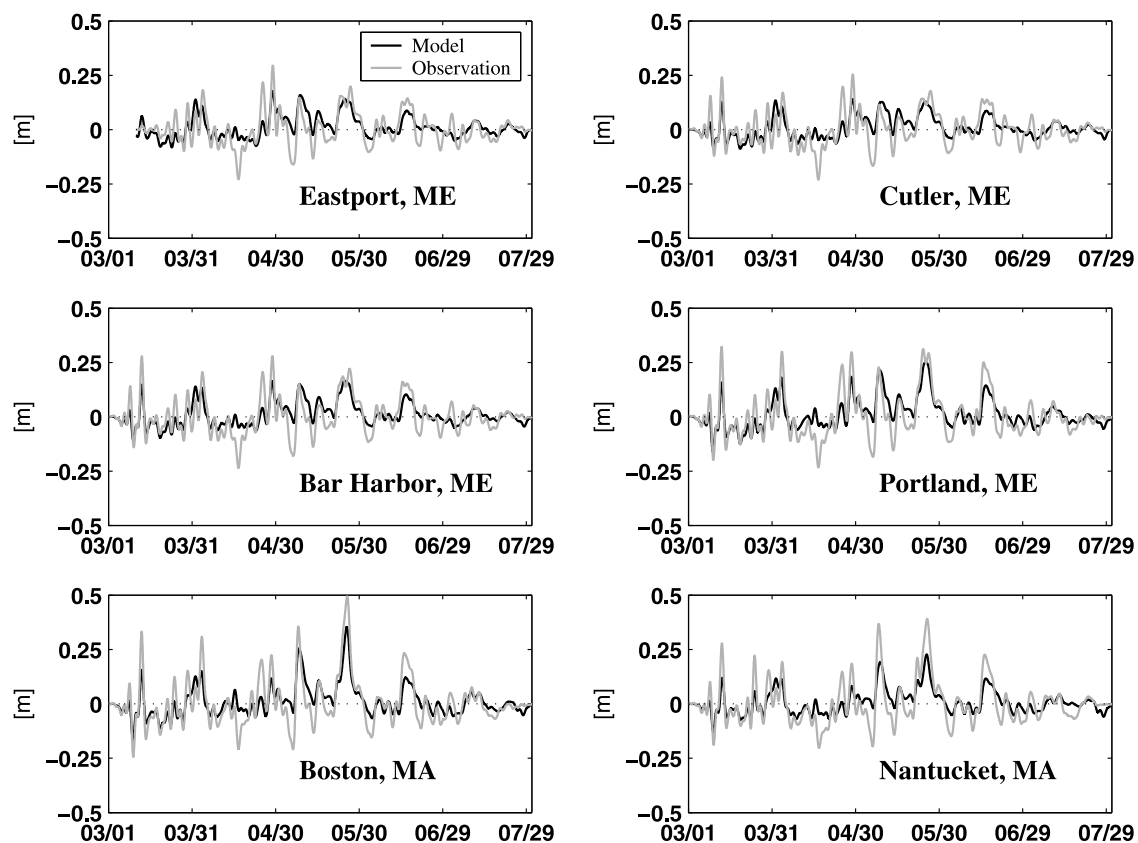
### 3. Model Results: Central Hindcast Simulation

[16] Standard circulation state variables (sea level, currents, temperature, and salinity) and *A. fundyense* cell concentration were archived at 6-h intervals. Interested readers are referred to an online animation showing the spatial and temporal evolution of modeled sea level, surface current, surface temperature and salinity fields, and surface *A. fundyense* cell concentration ([http://science.whoi.edu/users/ruoying/Redtide\\_05/Papers/avg\\_fields.avi](http://science.whoi.edu/users/ruoying/Redtide_05/Papers/avg_fields.avi)). Both simulated physical and biological fields display extremely complex spatial and temporal variability, highlighting the synergy between a numerical model and observations in the study of coastal ocean processes.

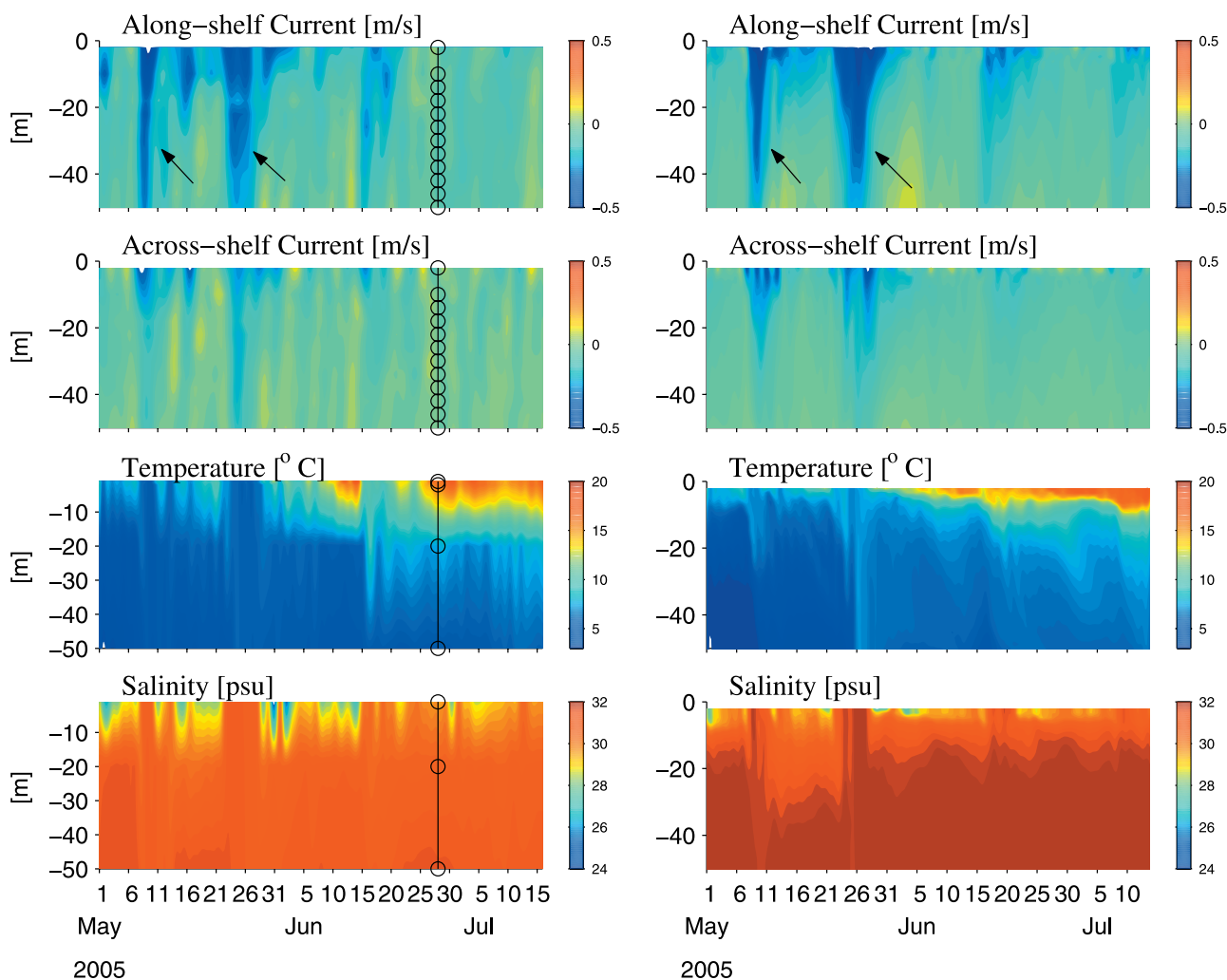
[17] Because the transport of material properties in the coastal region is largely determined by subtidal circulation, the fidelity of our hindcast model in reproducing subtidal variability is examined here. (Note that the modeled tidal characteristics are satisfactory, but will not be shown here for brevity.)

[18] Sea level comparisons (Figure 4) were made at 6 coastal sea level gauges, where both modeled and observed sea levels were 36-h low-pass filtered to remove tidal variability. It was found that the model is able to resolve subtidal sea level variations reasonably well, with correlation coefficients above 0.82 at all 6 stations. The model generally underestimates the magnitude of observed sea level variability, probably owing to insufficiency of surface wind-forcing, which is on a relatively coarse 40 km grid.

[19] Model-data comparisons were also made at where Gulf of Maine Ocean Observing System (GoMOOS) mooring data were available. For instance, at GoMOOS buoy B (50-m isobath), the circulation model is able to reproduce the coastal current and transport reasonably well (Figure 5). In particular, three strong southward transport events (two in May and one in June) due to the respective northeaster storms are all captured by the model. The model tracks observed temperature and shows the same seasonal warming trend. Note that the thickness of the observed thermocline in Figure 5 is determined by the coarse vertical spacing of the temperature sensors on the mooring, so it is not possible to evaluate the thermocline structure produced by the model. The simulated and observed salinity perturba-



**Figure 4.** Comparisons of observed (gray line) and modeled (black line) subtidal sea levels at six coastal gauges in the GOM.



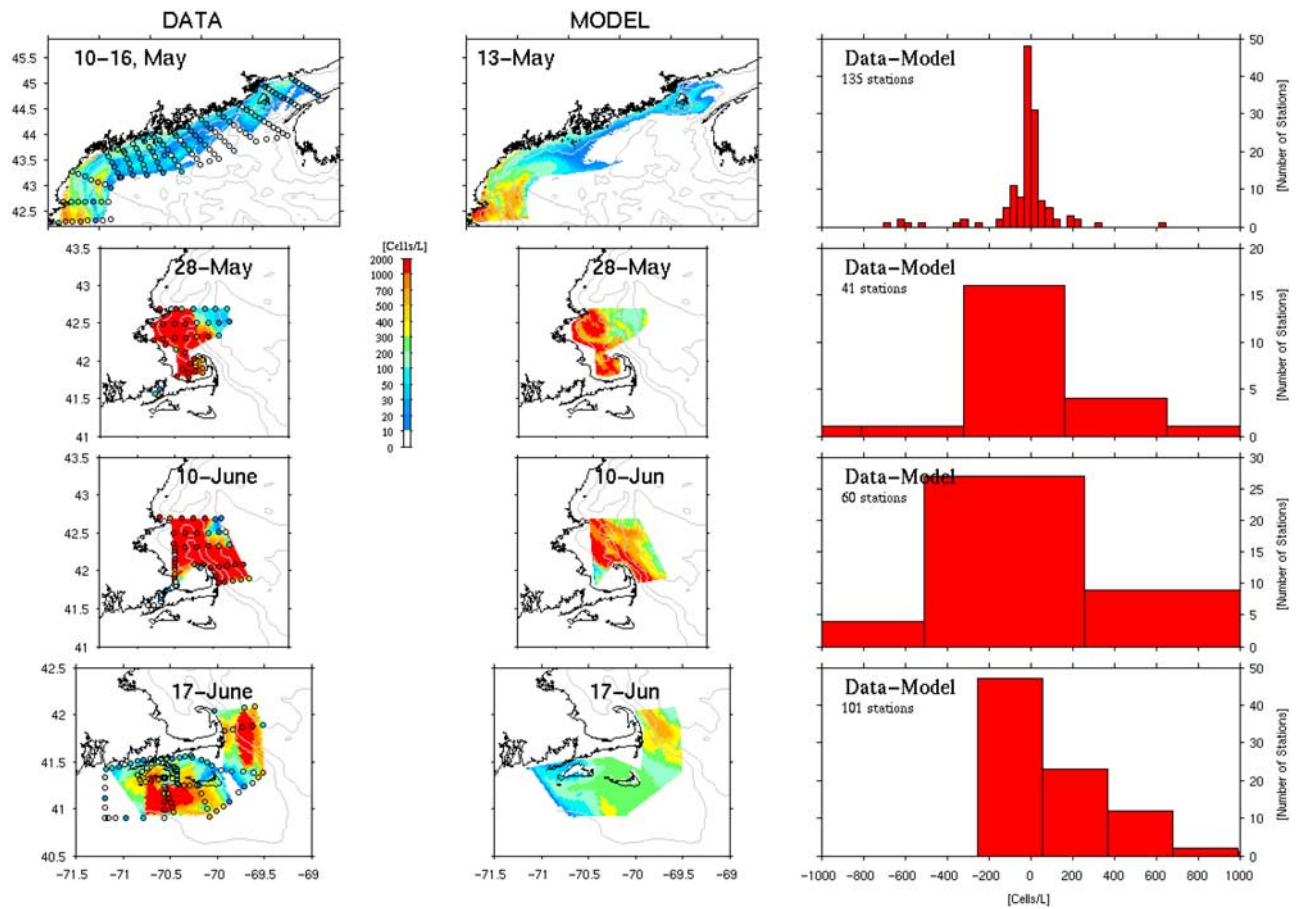
**Figure 5.** Comparison of (left) observed and (right) simulated time series at GoMOOS mooring B. For both sets, from top to bottom are depths profiles of across-shelf current, along-shelf current, temperature, and salinity. Circles in the left-hand panels indicate locations of current and temperature/conductivity sensors on mooring B. Three major transport events in May and June are indicated by arrows in both observed and simulated along-shelf current fields.

tions are also similar, testifying the model is capable of resolving significant influence from river runoff. One deficiency of the model solution is a  $\sim 1$  psu offset between the simulated and observed salinity fields. We found the origin of this offset lies in the model's initial and boundary conditions. Because NA-HYCOM does not account for coastal freshwater input well, the initial salinity field taken from the HYCOM best estimation on 1 March 2005 is biased. It is our understanding that HYCOM group is working to correct this salinity bias and will release a new set of reanalysis product in the near future (E. Chassignet, personal communication, 2007). The new HYCOM field should allow us to improve GOM salinity simulation. An alternative means for improvement is to correct such biased initial fields via assimilating in situ temperature/salinity observations. We will report this effort in a future communication. Nevertheless, these model-data comparisons suggest the circulation model is in general capable of reproducing observed circulation patterns, lending confi-

dence that the biological model is couched in a realistic physical environment.

[20] To validate the *A. fundyense* population dynamics model, direct comparisons were made between simulated and observed surface cell concentrations (Figure 6). In situ cell observations were collected during several gulf-wide and subregional-scale ship surveys from May through June 2005 [Anderson *et al.*, 2005]. To quantify model-data comparisons, we interpolated simulated cell concentration at each station where in situ cell counts were made, and computed a point-by-point model-data misfit for each pair of comparisons.

[21] Early in the season (10–16 May), observations show a high abundance of cells in the western GOM, with highest concentrations south and east of Cape Ann (see its location in Figure 3). A patch of high cell concentration was also present in the offshore water southeast of Casco Bay. In the eastern GOM, cell concentration around the Grand Manan Island was also significant ( $\sim 200$ – $300$  cells per liter). However, there were few/no cells in the coastal region



**Figure 6.** (right) Comparison of (left) observed and (middle) simulated surface *A. fundyense* cell concentration. In situ cell counts were collected by in situ ship surveys in May and June 2005.

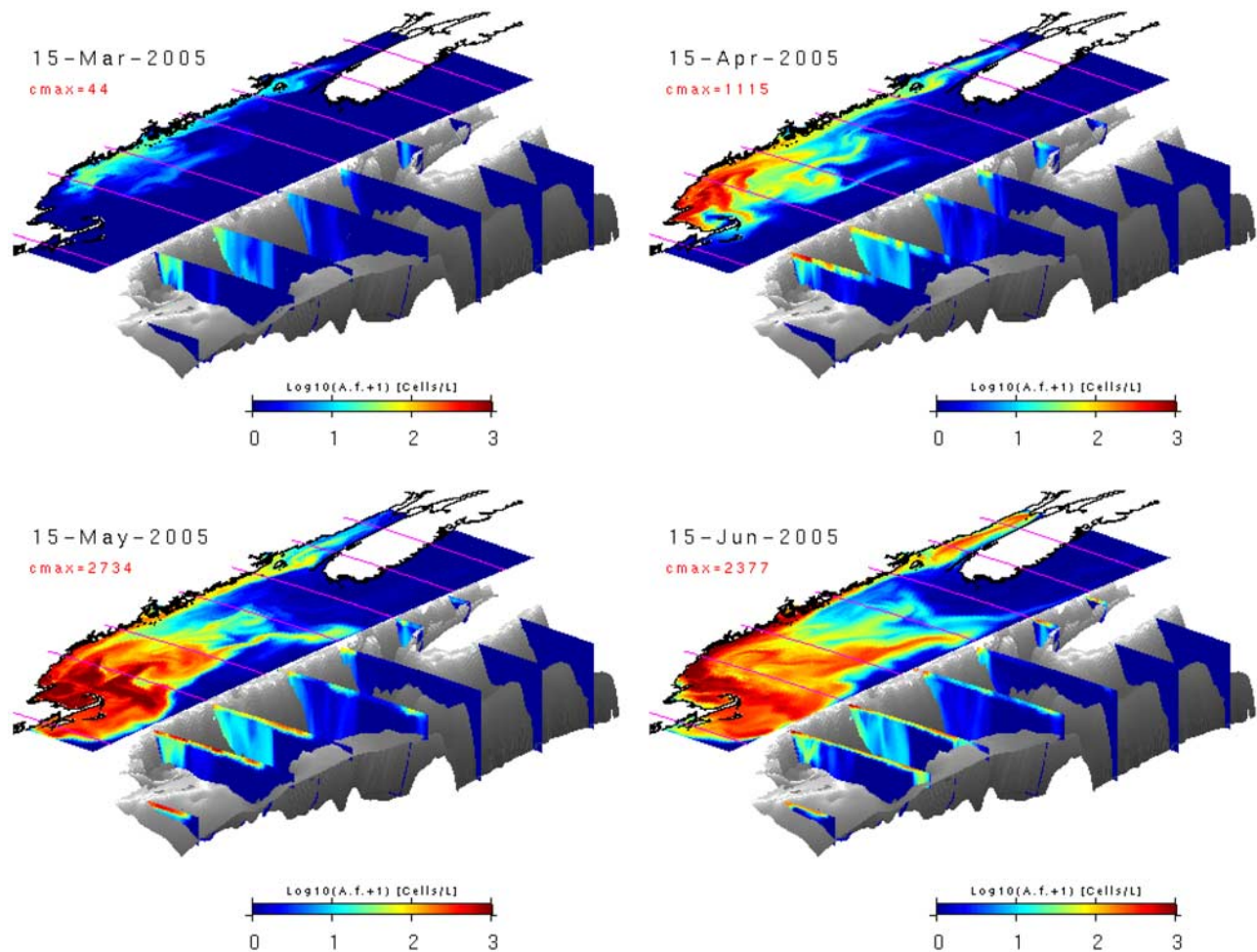
south of Nova Scotia, indicating the *A. fundyense* population did not have an upstream source from Scotia shelf water during this bloom event. The simulated cell concentration (sampled on 13 May) displays similar large-scale spatial distribution. The misfit calculation indicates simulated and observed cell abundances are consistent within  $\pm 50$  cells/L at 70% of the 133 stations. Some discrepancies are seen, including the model overestimation or underestimation in various regions in the GOM. But given the environmental uncertainties and the temporal aliasing of observations, we may conclude that the *A. fundyense* population dynamics model works reasonably well during this initial phase of the bloom.

[22] Subsequent subregional observations show abundant cell populations were inside Massachusetts and Cape Cod Bays by May 28. Relatively few cells were present in the easternmost stations offshore of Cape Ann. The simulated bloom reproduces the same spatial pattern with consistent cell concentration at more than 50% of the stations. The model tends to overestimate offshore and underestimate in the Bays. Two weeks later (June 10), observations indicate a similar pattern in Massachusetts Bay, and expansion of the bloom in the offshore region. Additional transects east of Cape Cod document the presence of the bloom in that area as well. The model captures this overall spatial distribution, although it underestimates the concentration at most of stations. By June 17, observations adjacent to Cape Cod show two large patches of high concentration were present,

one to the east of Cape Cod, and the other to the south of Martha's Vineyard and Nantucket Islands. Coincidentally, the model indicated elevated cell concentrations in the same two areas, although the absolute cell abundance was significantly underestimated. Recall these areas are in the vicinity of GOM ROMS open boundaries (Figure 1), so the treatment of *A. fundyense* open boundary conditions (section 2.2) may contribute to the model underestimation. In summary, all of these direct model-data comparisons demonstrate our bloom hindcast is able to track the temporal evolution and large-scale spatial structures of 2005 *A. fundyense* bloom during its initial and development phase. The model generally underestimates the bloom intensity, and like any regional models, solutions near model boundaries are subject to insufficiency of OBCs specifications, which may lead to large discrepancies with observations. (The statement here applies to biology sub-model, and simulated *A. fundyense* field only. Modeled hydrodynamic fields near GOM ROMS open boundary are in fact satisfactory because the shelf-scale ROMS provided dynamically consistent and numerically accurate boundary information for GOM circulation hindcast.)

[23] With the space-time continuous model realizations, we now depict the evolution and three-dimensional spatial structure of the 2005 bloom (Figure 7). On 15 March, *A. fundyense* was present in very low concentrations ( $< 50$  cells/L). These cells were largely confined in the coastal region between Casco Bay and Penobscot Bay, as





**Figure 7.** Temporal and three-dimensional spatial evolutions of simulated bloom conditions on 15 March, 15 April, 15 May, and 15 June. In each panel, surface cell concentration map is shown on top of seven GOM sections showing vertical cell distributions. Note that for better visualization, both surface and vertical cell concentrations are scaled by in  $\log_{10}$ .

well as in the Bay of Fundy, near to the areas of highest cyst abundance (see Figure 3, top). As the germination input increases and vegetative growth proceeds, cell concentration increased 25-fold a month later (by 15 April). The largest concentrations were south of Penobscot Bay, with a significant number of cells having entered Massachusetts Bay. Vertical sections reveal that cells recently germinated from the cyst bed off the western GOM coast were fueling the surface bloom further downstream. Vegetative cells were concentrated in the upper water column, where light is abundant and temperature is warmer. By 15 May, even more cells were present with maximum cell concentrations close to 3000 cells/L. By this time, the bloom had covered Massachusetts and Cape Cod Bays, and extended to the offshore water to the south and east, the Cape Cod, Martha's Vineyard, and Nantucket. With the connection of the southward moving Maine Coastal Current [Lynch *et al.*, 1997], much of the New England coast (with the exception of Rhode Island and Connecticut) was exposed to the massive bloom. By 15 June the bloom had expanded further, although the maximum cell concentration had begun to decrease. The transport by regional coastal circulation advected cells along the periphery of Georges Bank. While

the *A. fundyense* bloom in the western GOM had begun to decay, the bloom in the eastern GOM and the Bay of Fundy had started intensifying. This seasonal shift of the bloom or the pattern of PSP from west to east through time is consistent with previous observations [Anderson, 1997; Townsend *et al.*, 2001] and model simulations [McGillicuddy *et al.*, 2005]. A few weeks later, cell concentration started decaying gulf-wide, and by 30 July (not shown), *A. fundyense* cells were essentially gone from the nearshore coastal waters, signaling the end of the bloom season.

#### 4. Model Results: Sensitivity Experiments

[24] Given that the coupled model can produce a generally credible hindcast of the 2005 bloom, it can be used as a basis to investigate the relative importance of the three causative factors suggested by Anderson *et al.* [2005]. A set of model sensitivity experiments (Table 2) were executed to examine these hypotheses. In each case, one aspect of the model was changed and the results were compared with the central hindcast, relative to observations. The nature of the differences provides a means to assess the relative importance of each potential controlling parameter.

**Table 2.** Summary of Model Sensitivity Experiments

Run ID	Cyst Map	Wind-Forcing	River Discharge
Central Hindcast	2004	2005	2005
Sensitivity 1: Source	1997	2005	2005
Sensitivity 2: Wind	2004	2004	2005
Sensitivity 3: Rivers	2004	2005	2004
Sensitivity 4: Source	2004 BOF	2005	2005

#### 4.1. Twin Experiment 1: Initial Cyst Abundance

[25] To test whether initial cyst abundance was important for the 2005 bloom, a twin model experiment (with respect to the central hindcast presented above) was performed in which we utilized cyst observations collected by a gulf-wide survey in fall 1997 instead of the fall 2004 cyst survey. (Note that the BOF cyst observations in the map labeled 1997 come from surveys of the Bay of Fundy in 1981 [White and Lewis, 1982], 1982 and 1983 (data provided by Jennifer Martin, DFO).)

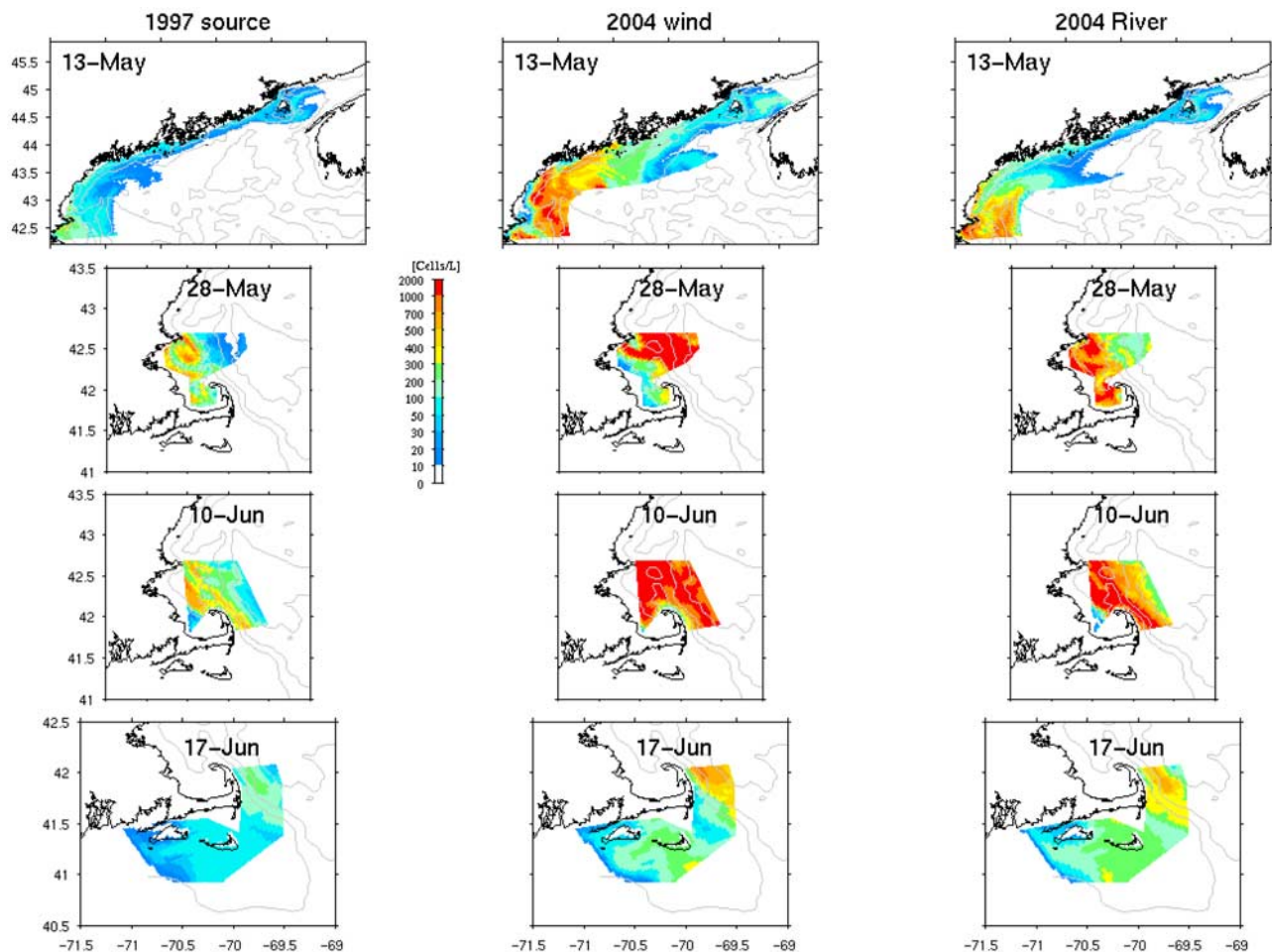
[26] Differences between cyst distributions in these 2 years are dramatic (Figure 3): relative to 1997, cyst abundance in 2004 increased by a factor of 2.4 in the Bay of Fundy, and by a factor of nearly 9 in the western GOM. Unfortunately, no cyst observations are available between 1997 and 2004 to

elucidate the reasons for such a dramatic change. (Anderson *et al.* [2005] suggest the increase of cyst abundance in the western GOM may have resulted from a large fall bloom of *A. fundyense* in 2004.)

[27] Using the 1997 cyst data, the hindcast model shows simulated cell concentrations that are at least fourfold smaller than the observation and the central hindcast (see Figure 8, left column, and Figure 6). Differences in bloom's spatial distribution are also apparent. On 13 May the offshore (southeast to the Casco Bay) patch of high-density cells is absent in the simulation using the 1997 cyst map as the inoculum. Although this model run shows bloom development in Massachusetts Bay by 28 May, both the spatial extent and intensity of the bloom are much too small compared to observations. Likewise, very few cells are present south and east of Cape Cod on 10 and 17 June, respectively in the simulation using 1997 cysts. All of these contrasting features (with respect to data and central hindcast) suggest high cyst abundance as a primary factor in the 2005 bloom.

#### 4.2. Twin Experiment 2: Surface Wind

[28] He and McGillicuddy [2008] showed that spring-summer surface wind conditions in 2005 were characterized



**Figure 8.** Simulated surface cell concentrations from three sensitivity model experiments. Modeled blooms are sampled on the same observation grid as shown in Figure 6. (left) Results from twin experiment 1 that using 1997 benthic cyst distribution; (middle) results from twin experiment 2 that using 2004 surface wind-forcing; and (right) results from twin experiment 3 that using 2004 river runoff data.

by anomalous northeasterlies relative to the southwesterly climatological winds. In order to examine if winds played a role in the massive 2005 bloom, a second twin model experiment was performed in which we replaced 2005 surface wind-forcing with NOAA EDAS 2004 surface wind-forcing. This choice of wind-forcing is justified on the basis that the mean wind in May 2004 was nearly identical to climatology [He and McGillicuddy, 2008].

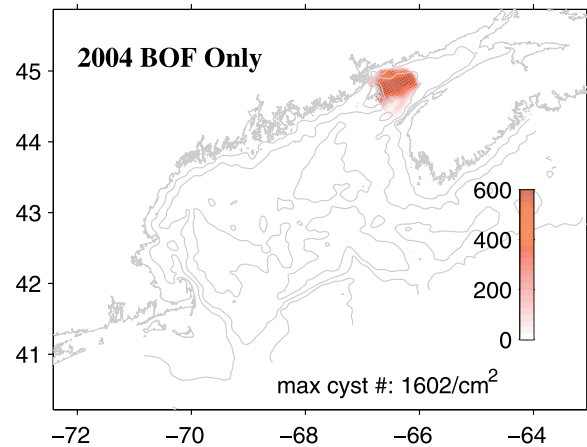
[29] Model solutions indicate that a massive regional bloom would have still occurred, although the upwelling favorable winds in 2004 would have pushed the bloom offshore and retarded its southward transport (see Figure 8, middle column, and Figure 6). In another words, had the wind conditions in 2005 been more typical, i.e., southwesterly, a less severe bloom would have resulted for nearshore regions, especially in Massachusetts and Cape Cod Bays (see for example the bloom distribution on 28 May). There would still have been a substantial *A. fundyense* population in offshore waters, however. This sensitivity experiment revealed that the episodic northeasterly winds and downwelling-favorable mean wind condition in 2005 led to stronger than normal onshore advection, which in turn significantly enhanced bloom intensity along the coast. Thus, winds in 2005 played an important role in modulating the development and distribution of the regional bloom.

#### 4.3. Twin Experiment 3: River Runoff

[30] River runoff into the Gulf was anomalously high in 2005 [Anderson et al., 2005; He and McGillicuddy, 2008]. In order to examine the impact of this river runoff anomaly on the bloom distribution, we conducted a third sensitivity experiment in which the 2005 river discharge data used in the central hindcast were replaced by river data from 2004. Our examination of the long-term USGS river discharge records shows that the runoff in 2004 was similar to the long-term mean, with a total spring-summer discharge volume about 50% of that in 2005.

[31] Comparisons with the central hindcast indicate that this sensitivity run produced only subtle differences in the spatial distribution and cell concentrations of the bloom (see Figure 8, right column, and Figure 6). Further examination of the simulated salinity field and *A. fundyense* concentrations reveals that the downwelling-favorable winds in 2005 induced strong onshore transport that confined the river plumes to the nearshore region. While enhanced local buoyancy due to larger river runoff accelerated the near-coastal flow and along-coast transport, the riverine influence on the large-scale bloom distribution was limited.

[32] An important caveat is that both the central hindcast and this river sensitivity experiment utilize the same climatological nutrient field. Therefore possible enhancement of nutrient delivery by river discharge was not addressed by these simulations. Anderson et al. [2005] suggested fresh water runoff could provide both macro- and micro-nutrients, including essential trace metals and organic materials that are known to be important growth factors for *A. fundyense* and other dinoflagellates [Prakash and Rashid, 1968; Gagnon et al., 2005]. We are unable to explore such effects using our model owing to the lack of river nutrient data.



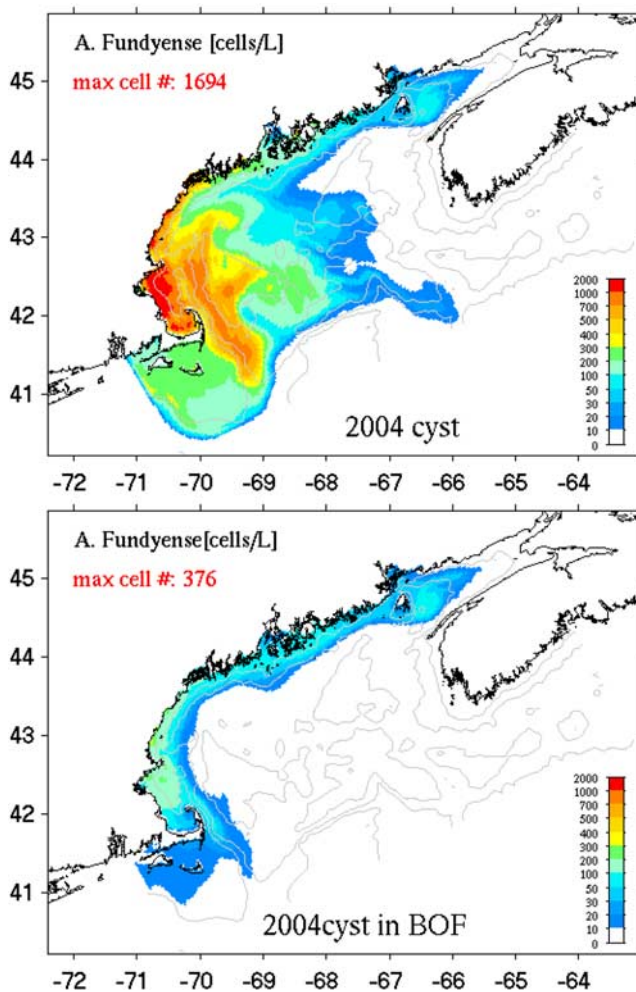
**Figure 9.** Artificial benthic cyst abundance data used in sensitivity experiment 4.

#### 4.4. Twin Experiment 4: Relative Importance of Cyst Beds—Bay of Fundy Versus Western GOM

[33] As we show in the previous section, cysts in both the BOF and western GOM were more abundant in fall 2004 than in prior years (Figure 3). Townsend et al. [2001] suggest that *A. fundyense* in the EMCC can be transported into the western GOM, and therefore *A. fundyense* populations originated in the Bay of Fundy could influence the entire GOM. Along the same lines, Keafer et al. [2005] identified a nearshore pathway (the Gulf of Maine Coastal Plume or GOMCP) for transport of cells from east to west. It is therefore of interest to differentiate the relative importance of the two main cyst beds in the cell distribution and abundance during the 2005 bloom. For this purpose, we carried out another sensitivity experiment in which an artificially constructed cyst map is used in the hindcast (Figure 9). Specifically, this cyst field has the same cyst distribution and abundance in the BOF as in the 2004 cyst map (Figure 3), but everywhere else in the GOM, the cyst abundance was set to zero. Therefore, this simulation tests whether the cysts in the BOF and the subsequent introduction of cells into the EMCC from that source are sufficient to cause the 2005 bloom without any further input of cells from “downstream” cyst beds near Penobscot and Casco Bays.

[34] Differences between this sensitivity experiment and the central hindcast are highlighted by comparing May monthly mean bloom conditions (Figure 10). Relative to the central hindcast, the bloom produced by this sensitivity experiment is much weaker. The maximum monthly mean cell concentration is an order of magnitude smaller than that produced by the central hindcast. Differences are also evident in the timing of the bloom. With the model animation, we tracked newly geminated BOF cells, some of which are entrained and transported by the Maine coastal currents to the southwest. We found it is not until the end of May that they finally reach Massachusetts Bay (not shown). In 2005, the bloom had already fully developed and reached its peak by that time. This time lag thus highlights the importance of the western GOM cyst bed in the massive bloom in 2005. Results here also support conceptual models presented by Anderson et al. [2005] and McGillicuddy et al. [2005]. Cells originating from the WGOM seedbed have a critical aug-





**Figure 10.** Comparison of May monthly mean cell concentration produced by (top) central hindcast and (bottom) twin experiment 4 that utilized artificial cyst abundance data (Figure 9).

menting effect on cell populations being transported from east to west in the GOM coastal current system.

## 5. Conclusions

[35] Our central model hindcast successfully reproduced the large-scale spatial distributions of *A. fundyense* populations observed in 2005. Point-by-point comparisons indicate that during the initial phase of the bloom, simulated cell abundances agree with observations within  $\pm 50$  cells/L at 90 out of 133 hydrographic stations. Comparisons with cell count data collected later in the season in the vicinity of Massachusetts and Cape Cod Bays as well as south and east of Cape Cod show the model still tracks the spatial distribution of the bloom, albeit with a consistent underestimation of cell abundance. One possible reason for this discrepancy is related to the cell mortality formulation in the model. Although the temperature-dependent mortality used herein was effective in capturing the demise of the bloom later in the season, it may be not optimal during the middle of the bloom season. Further refinement of the mortality representation is a topic of ongoing research. Another possible

explanation may be related to the nutrient field being used. Because the climatological nutrient database [Petrie *et al.*, 1999] was used in all of our model simulations, possible enhancement of macro- and micro-nutrients, including essential trace metals and organic materials important to *A. fundyense* growth, were not included.

[36] Model sensitivity experiments provide a means to distinguish the relative importance of three major factors contributing to the bloom. We found that the high abundance of cysts in the western GOM was the primary factor for the outbreak. Surface wind-forcing in 2005 was an important regulator, in the form of both episodic bursts of northeasterly winds and downwelling favorable mean conditions, causing strong onshore advection of offshore populations. The downwelling favorable winds also helped to accelerate the alongshore currents, transporting the cell population to the south and west more quickly, thereby affecting the timing of the bloom and the coastal areas being impacted. Even with “typical” winds in 2004, a bloom would still have occurred on a regional scale given the large number of cells provided as an inoculum from the abundant cysts. That bloom might not have had the same impact however, since delivery to shore is responsible for many of the most significant societal impacts of toxic *A. fundyense* blooms (e.g., nearshore shellfish harvesting closures). Model experiments also showed that high river runoff in 2005 produced more intense buoyant plumes that further enhanced along-coast transport of cells. However, these buoyant river plumes were confined near the coast by strong wind-induced onshore transport, and thus had limited impact on gulf-wide *A. fundyense* cell distribution.

[37] Collectively, our model results suggest that cyst abundance is the most important factor controlling the magnitude of the bloom. Monitoring of benthic cyst distributions could therefore provide a basis for interannual predictions in overall bloom severity. Apparently, other biological factors (germination, growth, mortality) as well as hydrodynamic transport play a major role in shaping the spatial and temporal structure of the bloom, as well as the intense patchiness characteristic of *A. fundyense* distributions. Deterministic predictions of those aspects will clearly require advanced observational infrastructure together with sophisticated techniques for data assimilation.

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D. M. Anderson and B. A. Keafer, Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.

R. He, Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, USA. (rhe@ncsu.edu)

D. J. McGillicuddy Jr., Department of Applied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.